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THE IMPORTANCE OF FIELD HYBRIDS IN DETERMINING SPECIES IN THE GENUS CEANOTHUS

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Every field botanist, having the faculty of careful observation, is repeatedly impressed with the number of apparent hybrids which occur in certain genera of seed-bearing plants. The genus *Ceanothus* is one of these genera. According to Katherine Brandegee, Dr. C. C. Parry was the first to call attention to the prevalence of natural hybrids in this genus. Mrs. Brandegee in her "Studies of Ceanothus" (1894) discussed the various hybrids which she had observed in the field and herbaria. She was of the opinion that most of the hybrids between members of the same section were fertile but she gave no supporting evidence. She stated that, "The only infertile hybrid, within its section, known to me is No. 69, *C. incanus* × *papillosus*. In this the ovaries are more or less abortive and no fruit was formed." If we accept the sterility test for distinct biological species, the two parents, *C. incanus* and *C. papillosus,* in this cross belong to two different species complexes (cenospecies of the experimentalist). John Thomas Howell (1940a) presents the case of hybridization between certain species of the section *Cerastes*. His conclusion is worthy of note: "My general conclusion is that anyone, interested in the taxonomy and the possible evolution of entities in the subgenus *Cerastes* of *Ceanothus,* cannot disregard the probable effect of hybridization, and that some of our puzzling entities can be more definitely limited as taxonomic units with the proper study and interpretation of intermediates of suspected hybrid origin." Many botanists have been reluctant to accept the importance of hybridization in the evolution of the numerous forms of *Ceanothus* and some ignore it entirely. However, anyone who has done much serious field study of this genus will come to agree with Howell's general conclusion.

It is the opinion of the writer that the number of true biological species (ecospecies of the experimentalist) existing at a given time in any genus of plants cannot be known until extensive experimental studies for testing the fertility of hybrids can be carried out. Until more logical methods for the determination of true biological or distinct species are set forth, botanists will do well to test out the numerous variants within a genus by putting them through the biological sterility sieve advocated by Clausen, Keck, and Hiesey (1939) shown in table 1.

Table 1. *The concept of species.*

Degree of separation: Internal / External	Hybrids fertile, second generation vigorous	Hybrids partially sterile, second generation weak	Hybrids sterile or none
In different environments	Distinct *subspecies* ECOTYPES	Distinct *species* ECOSPECIES	Distinct *species complexes*, CENOSPECIES
In the same environment	*Local variations* of one species BIOTYPES	Species overlapping in common territory (with hybrid swarms)	

Experimental methods require much time and labor, and it is evident to botanists who study woody plants that the adoption of the experimental method will be slow, and until such adoption other methods now employed by workers will continue to be used. However, by being aware of the importance of experimental methods, field workers will become more alert to the existence of natural hybrids and to geographic and ecological variations. By recognizing field hybrids and applying to them the same principles used by Clausen, Keck, and Hiesey in determining experimentally cenospecies, ecospecies, ecotypes, and biotypes, it has been possible to gain much helpful information in determining species complexes (cenospecies), distinct or biological species (ecospecies), subspecies (ecotypes), and local variations (biotypes) in the genus *Ceanothus*.

In this genus there are two rather well-defined sections or sub-genera, *Euceanothus* with leaves alternate and fruit not horned, and *Cerastes* with typically opposite leaves and horned fruit (Plate 28). In a recent publication, by Van Rensselaer and the writer (1942) the *Euceanothus* section includes thirty-three binomials (so-called species), seventeen trinomials (varieties), many minor variations, four named natural hybrids, and many other hybrids.

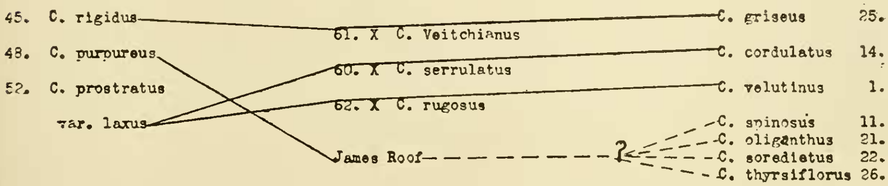
The *Cerastes* section includes twenty-three binomials, nine trinomials, many minor variations, four named natural hybrids, and other hybrids. Three named natural hybrids between members of the two sections are also included. The writer believes that the number of existing distinct species (ecospecies) is much fewer than represented by the number of binomials given in manuals, and that more subspecies (ecotypes) and local variations (biotypes) will be recognized when sufficient knowledge of the behavior of the hybrids is known. Some of this behavior can be learned by careful observation in the field.

INTERSECTIONAL HYBRIDS

If observed hybrid plants fail to set fruit year after year, one may assume with some degree of certainty that they are sterile, and that their parents belong to distinct species complexes (cenospecies). This situation is partially

CHART 1

Natural Hybrids between Species
of the Sections Cerastes and Euceanothus



exemplified in the intersectional cross between *C. prostratus* and *C. cordulatus* which has been given the designation × *C. serrulatus*. This hybrid was first collected in 1926 from a small colony of not more than four or five plants in a shallow draw on a ridge between Emerald Bay and Cascade Lake, Eldorado County, California. To my knowledge it has never been found at any other locality. It appears that a single hybrid plant may have been formed and that the other plants have resulted from natural layering. The evidence for considering the two parents of this hybrid as belonging to different species complexes would be more conclusive if more sterile hybrid plants were known. Associated with this hybrid is *C. prostratus*, *C. cordulatus*, and *C. velutinus*. The prostrate habit and the presence of sunken stomatal pits on the underside of the leaves relate it to *C. prostratus*, but the predominantly thinner and alternate leaves, the small deciduous stipules, and short racemose flower clusters relate it to *C. cordulatus*. The presence of both opposite and alternate leaves and the very pale blue to nearly white flowers seem to be intermediate characters. The plants have never been known to set fruit.

Two other field hybrids and six garden hybrids have been observed by the writer between members of the two sections (Chart 1). Only one of these hybrids, the garden hybrid *C. James Roof*, has ever been known to set fruit. The seeds of this hybrid when tested failed to germinate. The parents were *C. purpureus* and probably one of the following: *C. oliganthus*, *C. spinosus*, *C. thyrsiflorus,* or *C. sorediatus.* The two other observed field hybrids between members of the two sections are × *C. rugosus* and × *C. Veitchianus.* × *Ceanothus rugosus* appears to be a hybrid between *C. prostratus* and *C. velutinus.* Specimens have been obtained from two localities, one from the lava beds near Egg Lake, Modoc County, California, and the other from near Truckee, Nevada County, California. M. S. Baker and F. P. Nutting collected the specimens from Modoc County in 1894. Baker in a note states that the plant was a "decumbent form of *C. velutinus*—probably a hybrid of *C. prostratus* and *C. velutinus.*" The specimens from Truckee were collected by C. F. Sonne in 1890. Sonne reported that the plant sets flowers sparingly and that it does not fruit at all. It would seem then, that the two parents, *C. prostratus* and *C. velutinus,* definitely belong to different species complexes.

× *Ceanothus Veitchianus* appears to be a hybrid between *C. griseus* and probably *C. rigidus.* To my knowledge it was first collected by William Lobb in California, probably near Monterey where *C. griseus* and *C. rigidus* grow. Lobb probably collected seeds from *C. griseus* and *C. rigidus* and from this collection appeared the hybrid × *C. Veitchianus* in the Veitch and Sons nurseries of Exeter and Chelsea, England. I have seen no specimens collected from the field. The few garden hybrids of × *C. Veitchianus* which I have observed have never set fruit. It would appear from the sterility test that *C. rigidus* and *C. griseus* belong to different species complexes.

The genetic barrier between the two sections must be something more than chromosome number, because the diploid number for all species examined in the two sections by Nobs (1941) is 24 (Plates 29 and 30). Nobs also examined six hybrid plants of different parentage and all were found to have the same number of chromosomes as the parents, namely $2n = 24$.

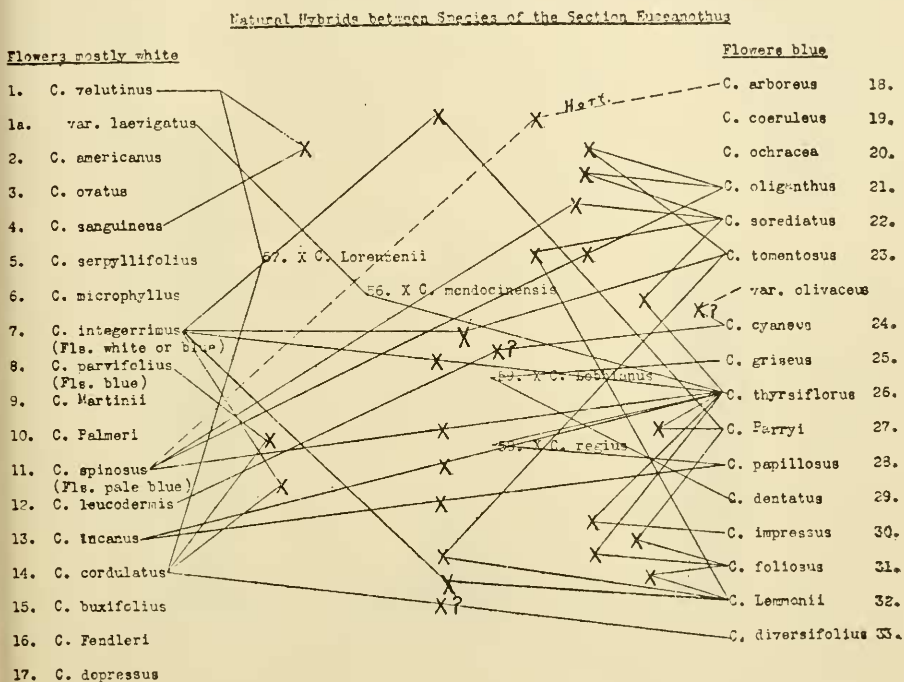
INTRASECTIONAL HYBRIDS

If observed hybrid plants are partially sterile and set fruit which produce seeds that germinate poorly or whose seeds produce a weak second generation, we may assume that the hybrid plants were produced by the crossing of distinct species (ecospecies of the experimentalist). If the hybrids proved to be fertile and the second generation vigorous, we may then assume that their parents belonged to distinct subspecies (ecotypes of the experimentalist) or that they were local variations of one species (biotypes of the experimentalist), depending upon whether they occurred in different environments or in the same environment. Examples of such hybrids have been observed many times in the field between members of the same section of the genus wherever they overlap in their distribution.

SECTION *Euceanothus*

In the section *Euceanothus,* the evidence from hybridization points toward the existence of more cenospecies and ecospecies than in the section *Cerastes.* In this section (*Euceanothus*) hybrids have been observed between most of the species that occupy the same area and that flower at the same time. In some cases where two species, as *C. cordulatus* and *C. diversifolius* or as *C. thyrsiflorus* and *C. incanus,* occur together only an occasional hybrid plant is formed and that plant usually appears to be totally sterile. In these cases we may assume that *C. cordulatus* and *C. diversifolius* belong to different species complexes (cenospecies) and also that *C. thyrsiflorus* and *C. incanus* belong to different species complexes. Since neither *C. cordulatus* nor

CHART 2



C. diversifolius are ever found in nature growing with either *C. thyrsiflorus* or *C. incanus,* no evidence from field hybrids has been obtained regarding their interrelationships. From morphological characters it would seem that *C. cordulatus* and *C. incanus* belong to the same species complexes, and that that complex is different from the one to which *C. thyrsiflorus* or the one to which *C. diversifolius* belongs.

In the natural hybrids observed between *C. cordulatus* and *C. velutinus* and between *C. thyrsiflorus* and *C. papillosus* on the other hand, many variations occur which appear to be only partially sterile and which appear to be members of a hybrid swarm, thus indicating that probably these two entities are distinct species (ecospecies). If these hybrids were quite fertile and their second generation vigorous, more local variations would be expected than are now found, and then these four entities would be considered subspecies (ecotypes) or local variations of one species (biotypes), depending upon whether they normally occurred in different environments or in the same environment. Most of the other crosses observed in the *Euceanothus* section, and recorded in chart 2, appear to follow the same general patterns as given in the examples just cited.

A summary of the recorded natural hybrids in this section shows a total of thirty, involving twenty-one species. *Ceanothus thyrsiflorus*, which in its distribution contacts more species than any other entity in the *Euceanothus* section, has entered into nine crosses, whereas the other species with fewer contacts have been involved in from one to five crosses. Three of the thirty crosses have been given hybrid binomial designations because they have been considered as species or varieties by other workers. One other hybrid has been named because of its presence in the nursery trade. Since much confusion exists in the literature about these hybrid entities, it seems worth while to give a brief account concerning them.

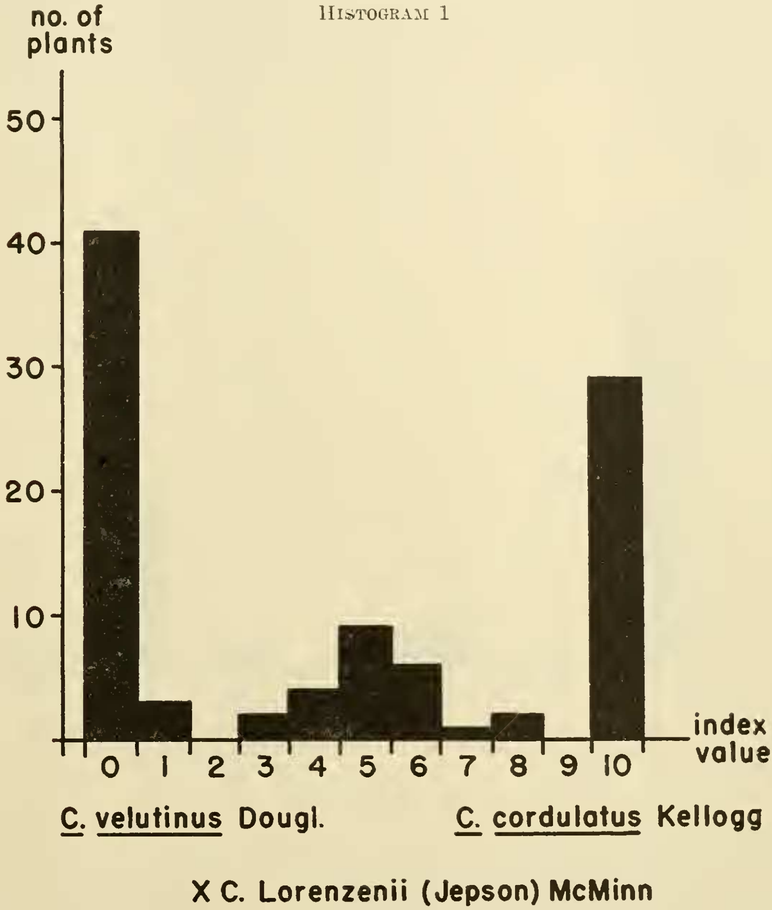
Named Hybrids of the Section *Euceanothus*

× *Ceanothus mendocinensis* appears to be a hybrid between *C. thyrsiflorus* and *C. velutinus* var. *laevigatus*. Plants of this cross have been collected in several scattered locations in Mendocino County, California, and in adjacent counties where the two parents overlap in their distribution. They usually occur as individual plants with one or both parents, never in colonies. The fertility of the seed has not been tested, but since so few plants have been found where the parents occur together, and since the hybrids appear to be rather uniform in those characters which are intermediate between those of the parents, it would appear that the plants were first-generation hybrids and that the parents belong to distinct species.

× *Ceanothus Lorenzenii* has been considered to be a variety of *C. velutinus* by some botanists. It occurs in the Sierra Nevada of California from Kern County northward to Siskiyou County and eastward in Nevada. Apparently this hybrid is the result of a cross between *C. velutinus* and *C. cordulatus* (Plate 31). Field studies made about five miles north of Markleeville, Alpine County, California, in the summers of 1941 and 1942, furnished the most convincing evidence. On an extensive old burned-over area there occurred *C. velutinus*, *C. cordulatus*, and *C. prostratus*. The hybrid plants were found only in areas where *C. velutinus* and *C. cordulatus* were closely associated. In areas where one species occurred to the exclusion of the other no hybrids were observed. Most of the hybrids resembled the species *C. velutinus* more than *C. cordulatus*. The stiff branches and smaller leaves without varnish above, however, gave evidence of the part *C. cordulatus* had in its origin. A few plants were found which resembled *C. cordulatus* more than *C. velutinus*. It appeared from the field studies that the hybrid plants were mostly sterile. If they were quite fertile one would expect more individuals intermediate between the two parents and the hybrid (Histogram 1). I believe most of the specimens of × *C. Lorenzenii* are first generation hybrids. Nobs, after field and cytological studies, also concluded that *C. velutinus* var. *Lorenzenii* Jepson is a hybrid between *C. velutinus* and *C. cordulatus* (Plates 32 and 33).

× *Ceanothus Lobbianus* is probably the result of a cross between *C. griseus* and *C. dentatus*. It was first grown in England from seed collected by William

Histogram 1



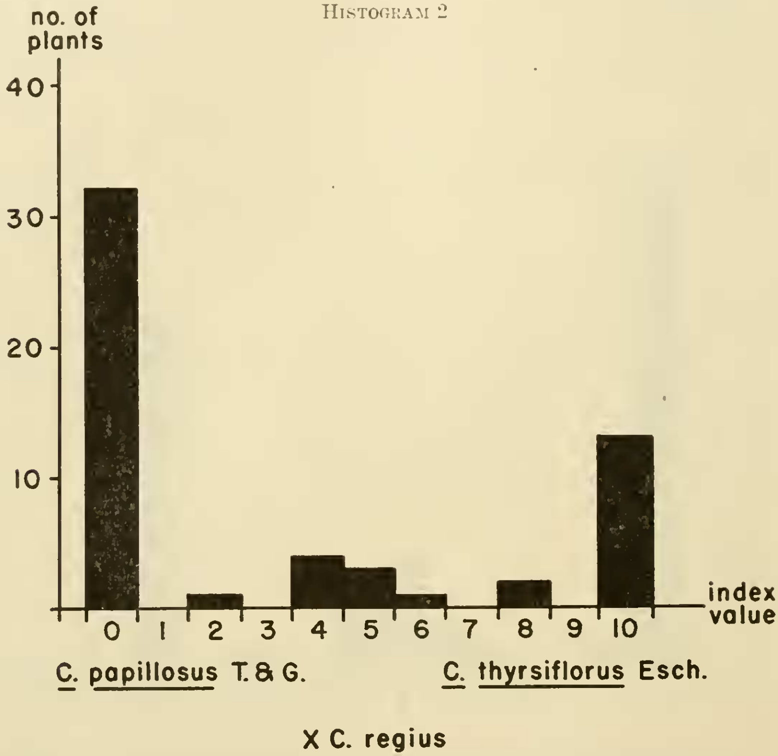
Histogram 1 represents the distribution of plants into 11 groups based upon an index value determined by studying 10 characters of *C. cordulatus*. The plants were taken from a random sampling in an area where *C. cordulatus* and *C. velutinus* overlapped in their distribution. Plants with all 10 characters were classified as *C. cordulatus;* plants with none of these characters were classified as *C. velutinus;* those with 4, 5, and 6 characters were classified as × *C. Lorenzenii;* and those with 1, 3, 7, or 8 characters are unnamed hybrids. No plant in the sampling was found with 2 or 9 characters. As the groups approach 0 the plants more closely resemble *C. velutinus*.

(× = hybrid)

Lobb in California, probably in the region of Monterey where *C. griseus* and *C. dentatus* occur. A few plants collected as natural hybrids in the Monterey region and now growing in California gardens approximate the type specimen of the original *C. Lobbianus*. Seeds have been collected from these hybrids but their fertility is not known. Since so few plants of this hybrid occur either in the wild or in any known garden collection it would seem that the hybrid is only partially fertile and therefore the parents, *C. griseus* and *C. dentatus*, belong to distinct species.

× *Ceanothus regius* is a hybrid between *C. thyrsiflorus* and *C. papillosus*. It has been observed several times wherever the two parents overlap in their

HISTOGRAM 2



Histogram 2 represents the distribution of plants into 11 groups based upon an index value determined by studying 10 characters of *C. thyrsiflorus*. The plants were counted from a random sampling in an area where *C. thyrsiflorus* and *C. papillosus* overlapped in their distribution. Plants with 10 characters were classified as *C. thyrsiflorus;* those with none of these characters were classified as *C. papillosus;* those with 4 or 5 characters were classified as × *C. regius;* and those with 2, 6, or 8 characters were classified as unnamed hybrids. No plant in this sampling was found with 1, 3, 7, or 9 characters.

distribution in San Mateo and Santa Cruz counties, California. The hybrids give evidence of being only partially sterile, consequently the parents belong to distinct species (Plate 34, and Histogram 2).

SECTION *Cerastes*

In the section *Cerastes* (those plants with typically opposite leaves) there appears to be more evidence for a greater number of subspecies and fewer species and species complexes. In this section, *C. cuneatus, C. Greggii,* and *C. prostratus* have wider ranges of distribution than any of the other entities and they have entered into more crosses than any of the others. Wherever *C. cuneatus* and *C. Greggii* and its vars. *vestitus* and *perplexans* overlap in their distribution, many intermediates occur which appear to be fertile. But since their degree of fertility is not known it is not possible to state whether the parents are in the nature of subspecies or species. In the crosses observed between *C. cuneatus* and *C. prostratus* the hybrid plants appear to be partially sterile, wherefore, their parents appear to be distinct species. At the present time no localities are known to the writer where *C. prostratus* and *C. Greggii* occur together. However, there is evidence in the southern middle Sierra Nevada of California that they may have overlapped in their distribution sometime in the past. In this area, particularly in Tuolumne and Calaveras counties, entities occur which seem to possess characters originating from both species. Two of these entities appear in some manuals as species binomials and are worthy of further consideration.

The apparently fertile entity known as *C. fresnensis* (Fresno Mat), occurs on the western slope of the Sierra Nevada between 3000 and 6500 feet elevation, from Fresno County northward to Tuolumne County or probably to Eldorado and Placer counties, mostly at the southern extension of the range of *C. prostratus.* In 1939 the writer gave the distribution of this rather baffling entity as extending from Fresno County northward to Plumas County. However, after becoming more aware of the presence of hybrids in this genus, extensive field studies were carried on during the summers of 1940, 1941, and 1942, and I am now of the opinion that some of the herbarium specimens studied from the more northerly localities had been taken from hybrid plants of *C. cuneatus* × *C. prostratus* and its variety *laxus,* and from *C. arcuatus. Ceanothus fresnensis* is entirely prostrate, while *C. arcuatus* and most hybrids between *C. cuneatus* and *C. prostratus* are usually intermediate between the two in habit of growth. That *C. Greggii* var. *vestitus* has entered into the origin of *C. fresnensis* is evidenced by the character of the pubescence and the nature of the fruit. *Ceanothus Greggii* var. *vestitus* now occurs in Kern, Inyo, and Mono counties and in the past may have overlapped in its distribution with *C. prostratus.* John Thomas Howell (1940) also considers the probability that *C. fresnensis* "is descended from the offspring of a fertile cross between *C. prostratus* and *C. vestitus*" (*C. Greggii* var. *vestitus*). If we accept an early hybrid origin of *C. fresnensis,* then *C. prostratus* and *C. Greggii* var. *vestitus* must have belonged to distinct subspecies.

The other apparent fertile entity previously referred to is *C. arcuatus.* It occurs in scattered localities from about 3000 to 7600 feet elevation on the western slope of the Sierra Nevada of California from Madera County northward to Plumas County. Near the summit on the south slope of Robb's Peak, Eldorado County, elevation 6500 to 6700 feet, it is one of the dominant shrubs associated with *Arctostaphylos patula* and *Ceanothus prostratus.* A few prostrate plants which appear to be *Ceanothus fresnensis* also occur in this association. These may be hybrids of *C. prostratus* and *C. arcuatus.*

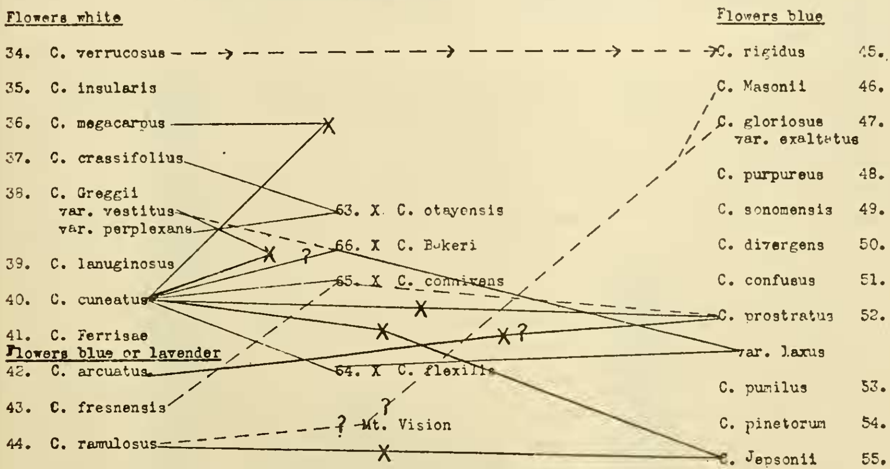
Ceanothus arcuatus seems to have segregated out of a hybrid population formed by the crossing of *C. cuneatus* with *C. fresnensis.* The habit of growth, character of fruit, and color of flowers are intermediate between the two probable parents. The grayish bark resembles that of *C. cuneatus* while the leaves resemble more those of *C. fresnensis.* In the Sugar Pine Ridge region along Highway 108, Tuolumne County, occur plants of *C. cuneatus* and *C. fresnensis* as well as hybrids between these two entities. At higher elevations along Highway 108 the hybrid form alone occurs. In Eldorado, Nevada, Placer, and Plumas counties, plants scarcely distinguishable from these hybrids occur in the Upper Transition and Canadian Life Zones far above the distribution of *C. cuneatus.* Since these plants are scarcely distinguishable from the hybrids of Tuolumne County and since they occur in a different geographical area in the absence of both *C. fresnensis* and *C. cuneatus,* I believe there are sufficient reasons for regarding them as belonging to a distinct subspecies or probably to a distinct species. It seems to me we have here a subspecies or a species which has "just arrived" and is now migrating northward from its center of hybrid origin.

The group of entities including *C. pinetorum, C. postratus* and its vars. *laxus* and *occidentalis, C. pumilus, C. confusus, C. divergens,* and *C. purpureus* has so many forms which appear to grade into each other that the entities may well exist as subspecies of one large polymorphic species. These entities are not only very closely related to each other but also to another smaller group composed of *C. rigidus, C. Masonii, C. gloriosus* and its var. *exaltatus.* The two groups differ slightly from one another in the character of the leaf margins. The former normally has leaves with serrate or spinulose margins, and the latter has leaves with dentate to quite entire margins. In the foothills of the Hood Mountain Range in Sonoma County, California, members of these two groups overlap in their distribution and have produced numerous hybrids, many of which appear to be fertile. Since the barrier between most of these entities appears to be that of geographic or ecologic isolation rather than genetic, it would seem that the entities are probably in the nature of subspecies. They seem to hybridize freely wherever they meet, but appear quite distinct in their own geographic ranges.

Ceanothus sonomensis of the Hood Mountain Range, Sonoma County, California, may be the result of the crossing of one of these hybrids with *C. cuneatus,* which occurs in the same area. This unit now occupies a small area somewhat isolated from the other forms of *Ceanothus* growing in that general region. When *C. cuneatus* is brought into the picture it brings in another series of forms which seems to hybridize with the others, and until experimental methods are used it would be unwise to make predictions as to the exact nature of the entities. That *C. sonomensis, C. arcuatus,* and several other somewhat similar entities in the section *Cerastes* might be the results of interspecific hybridization cannot be entirely ruled out. G. Ledyard Stebbins (1942a) has pointed out in his paper on the "Role of Isolation in the Differentiation of Plant Species" that occasionally recombinations should occur in the progeny of a partially sterile interspecific hybrid involving "small units genetically independent of morphological differences." He further states that "Some of these new recombinations could be fertile types which would be different in appearance from either of their original parents and exhibit partial intersterility with both of them. They would thus become the progenitors of new species."

CHART 3

Natural Hybrids between Species of the Section Cerastes



A summary of the recognized natural hybrids in the section *Cerastes,* as given in the book *Ceanothus,* gives a total of twenty-one, of which four are named and seventeen unnamed (Chart 3). The four named hybrids represent binomials which have appeared as distinct species in some publications. Eight so-called species of this section have entered into the hybrid complex. *Ceanothus cuneatus, C. prostratus,* and *C. Greggii* are the most widely distributed named entities and they have entered into crosses more often than any of the other named entities. *Ceanothus verrucosus,* a species with relatively few variations, to my knowledge has not entered into any natural cross. This species has a rather limited range of distribution in San Diego County, California, which does not overlap with the distributional ranges of other species in the same section. According to the concept of genetic homogeneity as reviewed by Stebbins (1942), we might consider that *C. verrucosus,* because of its limited distribution, is genetically homogeneous and that it consists of relatively few biotypes which in turn are relatively homozygous. On the other hand we might consider *C. cuneatus, C. prostratus,* and *C. Greggii,* since they are widespread species, as being heterogeneous in their genetic make up. This heterogeneity is well exemplified by the numerous biotypes which occur in these species.

Named Hybrids of the Section *Cerastes*

× *Ceanothus otayensis* in known only from Otay Mountain in San Diego County, California, and is here considered to have originated as the result of a cross between *C. crassifolius* and *C. Greggii* var. *perplexans*. Both of these entities occur together on Otay Mountain. The hybrid plants bear good fruit and the seeds appear to be fertile. If they are found to produce strong second generation plants, then the two parents, *C. crassifolius* and *C. Greggii* var. *perplexans*, must be considered to belong to different subspecies. One evidence for their fertility is the amount of variability which occurs among the hybrid plants.

The name × *Ceanothus flexilis* has been given to those hybrid plants occurring in northern Shasta, Lassen, and southwestern Modoc counties of California. In these localities *C. cuneatus* and *C. prostratus* var. *laxus* overlap in their distribution and they are considered to be the parents of × *C. flexilis*. The habit of growth, many leaf characters, size of fruit, and flower color are usually intermediate between the two parents. The fertility of the hybrids is not known, but from field observations I would suspect partial sterility. If the suspicion is proved to be a fact by experimental methods, then the parents, *C. cuneatus* and *C. prostratus*, belong to distinct species.

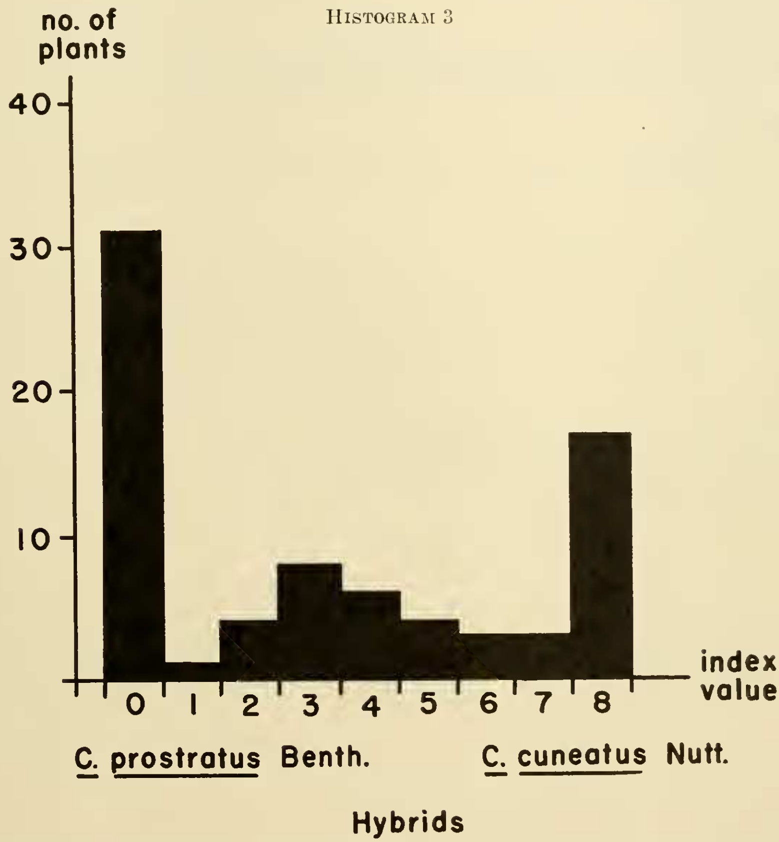
× *Ceanothus Bakeri* is another named hybrid which appears to have resulted from a cross between *C. prostratus* var. *laxus* and either *C. Greggii* var. *vestitus* or one of the many varieties of *C. cuneatus*. The single plant known to me of this hybrid was collected by C. F. Baker from Kings Canyon, Ormsby County, Nevada, in 1902. The three fragmentary specimens resemble somewhat specimens of × *C. flexilis* and × *C. connivens*, both of which probably have genes of *C. prostratus* in their makeup. This small bit of evidence would favor the assumption that *C. prostratus* and *C. Greggii* or *C. cuneatus* belong to distinct species.

Specimens representing the named hybrid × *C. connivens* were collected from near Sheep Ranch, Calaveras County, California, by E. L. Greene and by T. S. Brandegee. Field studies in the Calaveras-Sheep Ranch area in 1941 failed to disclose any specimens which quite resembled the specimens of the earlier collectors. However, in the Calaveras-Tuolumne area, where *C. cuneatus*, *C. prostratus*, and *C. fresnensis* grow, many hybrid plants occur, some of which appear much like × *C. connivens*. It is probable that × *C. connivens* represents a cross between *C. cuneatus* and either *C. prostratus* or *C. fresnensis*.

In concluding this paper mention should be made of the numerous other hybrid plants which occur between *C. cuneatus* and *C. prostratus* wherever these two species occupy the same local area (Plates 35 and 36 and Histogram 3). *Ceanothus cuneatus* is primarily a component of hard chaparral in the Upper

Sonoran Life Zone, while *C. prostratus* occurs chiefly in the open pine forests of the Transition and Lower Canadian Life Zones. However, along the none-too-well-defined borders of these life zones these two entities overlap in their distribution and also in their characteristics. Some of the hybrids observed appear to have good fruits and seeds; whether the seed produce strong and

HISTOGRAM 3



Histogram 3 represents the distribution of plants into 9 groups based upon an index value determined by studying 8 characters of *C. cuneatus*. The plants were taken from a random sampling in an area where *C. cuneatus* and *C. prostratus* overlapped in their distribution. Plants with 8 characters were classified as *C. cuneatus;* plants with none of these characters were classified as *C. prostratus;* and those with 1, 2, 3, 4, 5, 6, or 7 characters were classified as unnamed hybrids. Plants with a decreasing number of *C. cuneatus* characters possessed an increasing number of *C. prostratus* ones.

fertile offspring is not known. Since the hybrid forms do not vary as much as F_2 and F_3 offspring usually do from heterozygous parents, and since there are relatively few individuals compared to the number of individuals of both parents, I believe the hybrids are partially sterile and that their parents are distinct species.

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Van Rensselaer, M. and H. E. McMinn

1942, Ceanothus. Santa Barbara Botanic Garden, Santa Barbara.

I wish to express my sincere appreciation to Mr. M. A. Nobs and Mr. John Poindexter for furnishing the data and photographs for plates 29 to 36 and text figures 1 to 3.

EXPLANATION OF PLATES

PLATE 28

Section Euceanothus

A. Branchlet with alternate leaves, thin, early falling stipules, and umbel-like clusters of flowers in racemes.

B. Fruit without apical horns.

C. Cross section of leaf showing stomata protected by guard cells on lower surface.

Section Cerastes

D. Branchlet with opposite leaves, thick, corky, persistent stipules, and umbel-like fruit-cluster.

E. Fruit with apical horns.

F. Cross section of leaf showing stomata in sunken pits on the lower surface.

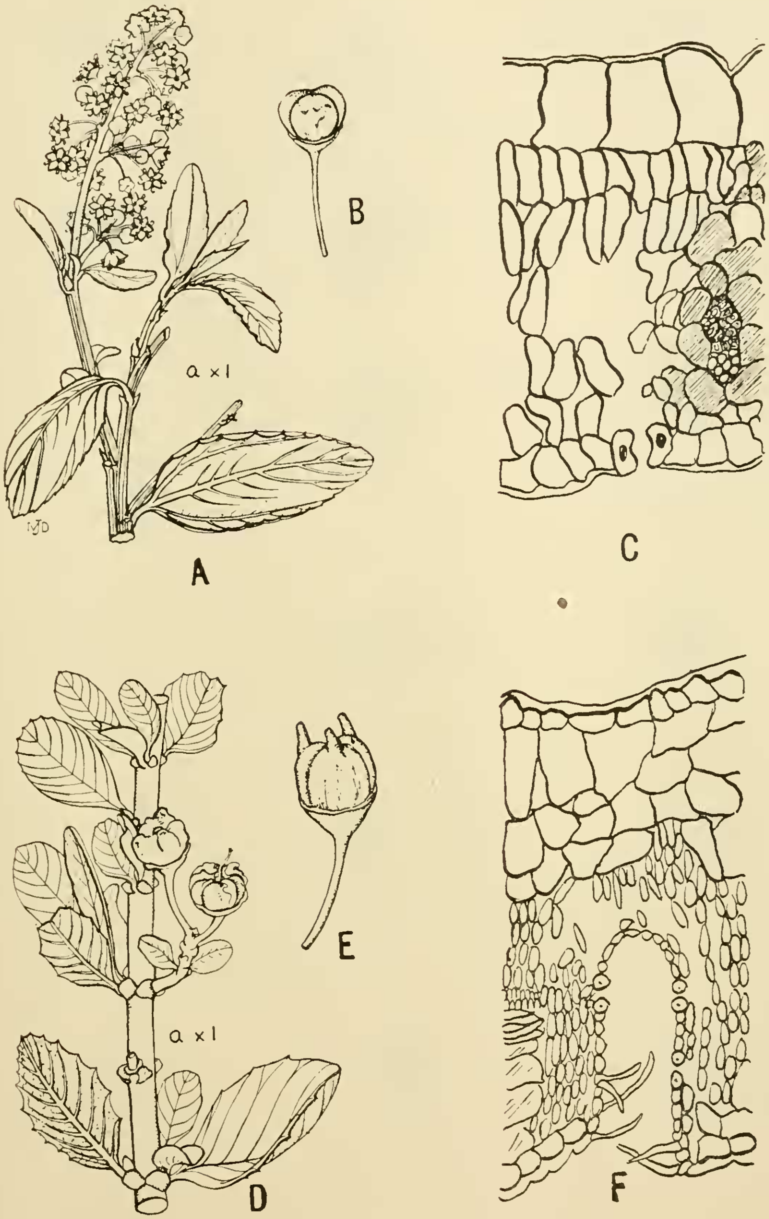

a ×1
A
B
C
a ×1
D
E
F

PLATE 29

Section Euceanothus

Fig. 1. *C. arboreus.*

Fig. 2. *C. cordulatus.*

Fig. 3. *C. cyaneus.*

Fig. 4. *C. foliosus.*

Fig. 5. *C. incanus.*

Fig. 6. *C. integerrimus* var. *californicus.*

Fig. 7. *C. Lemmonii.*

Fig. 8. *C. leucodermis.*

Fig. 9. *C. papillosus.*

Fig. 10. *C. Parryi.*

Fig. 11. *C. Parryi.*

Fig. 12. *C. thyrsiflorus.*

Fig. 13. *C. thyrsiflorus.*

Fig. 14. *C. tomentosus.*

Fig. 15. *C. velutinus.*

Fig. 16. *C. velutinus* var. *laevigatus.*

Fig. 17. *C. spinosus.*


Fig. 1


Fig. 2

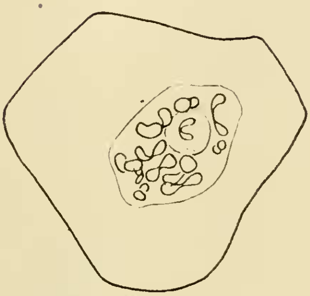


Fig. 3


Fig. 4


Fig. 5


Fig. 6


Fig. 7


Fig. 8


Fig. 9


Fig. 10


Fig. 11


Fig. 12


Fig. 13


Fig. 14


Fig. 15


Fig. 16


Fig. 17

PLATE 30

Section Cerastes

Fig. 1. *C. prostratus* var. *occidentalis.*

Fig. 2. *C. cuneatus.*

Fig. 3. *C. cuneatus.*

Fig. 4. *C. cuneatus.*

Fig. 5. *C. cuneatus.*

Fig. 6. *C. Ferrisae.*

Fig. 7. *C. gloriosus.*

Fig. 8. *C. prostratus* var. *laxus.*

Fig. 9. *C. prostratus* var. *laxus.*

Fig. 10. *C. prostratus.*

Fig. 11. *C. ramulosus.*

Fig. 12. *C. rigidus.*

Fig. 13. *C. rigidus.*

Fig. 14. *C. verrucosus.*


Fig. 1

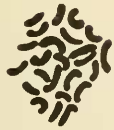


Fig. 6


Fig. 11


Fig. 2


Fig. 7


Fig. 12


Fig. 3

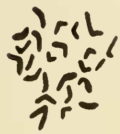


Fig. 8


Fig. 13


Fig. 5


Fig. 9


Fig. 14


Fig. 4

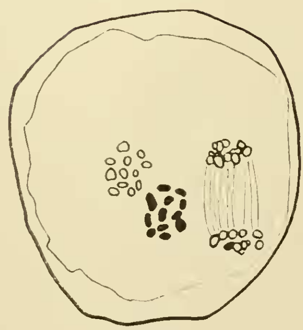
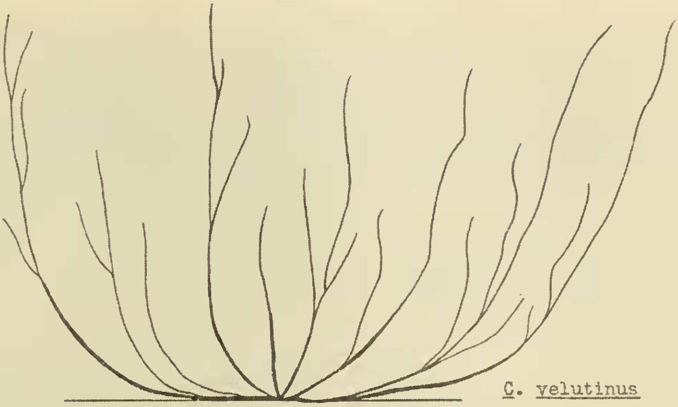


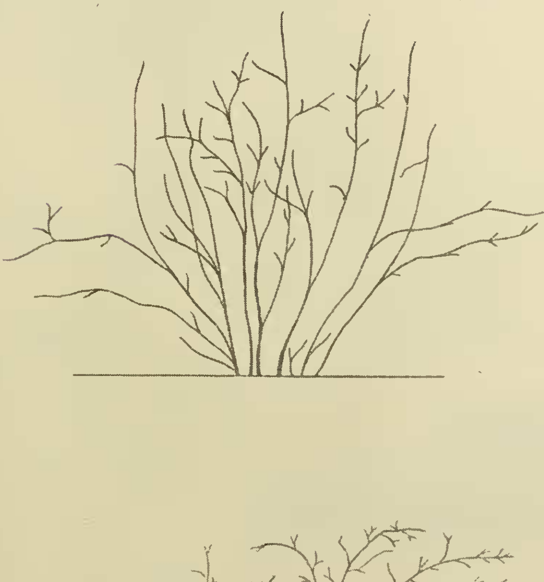
Fig. 10

PLATE 31

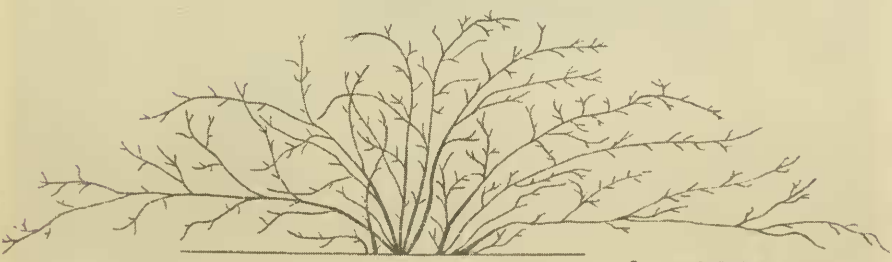
Diagrams of the growth forms of *C. velutinus*, *C. cordulatus*, and the hybrid × *C. Lorenzenii*.



C. velutinus



X C.Lorenzenii
(hybrid)



C. cordulatus

PLATE 32

Photographs of specimens of *C. velutinus*, *C. cordulatus*, and a graded series of five of their hybrids taken from an area where the two species occur together.

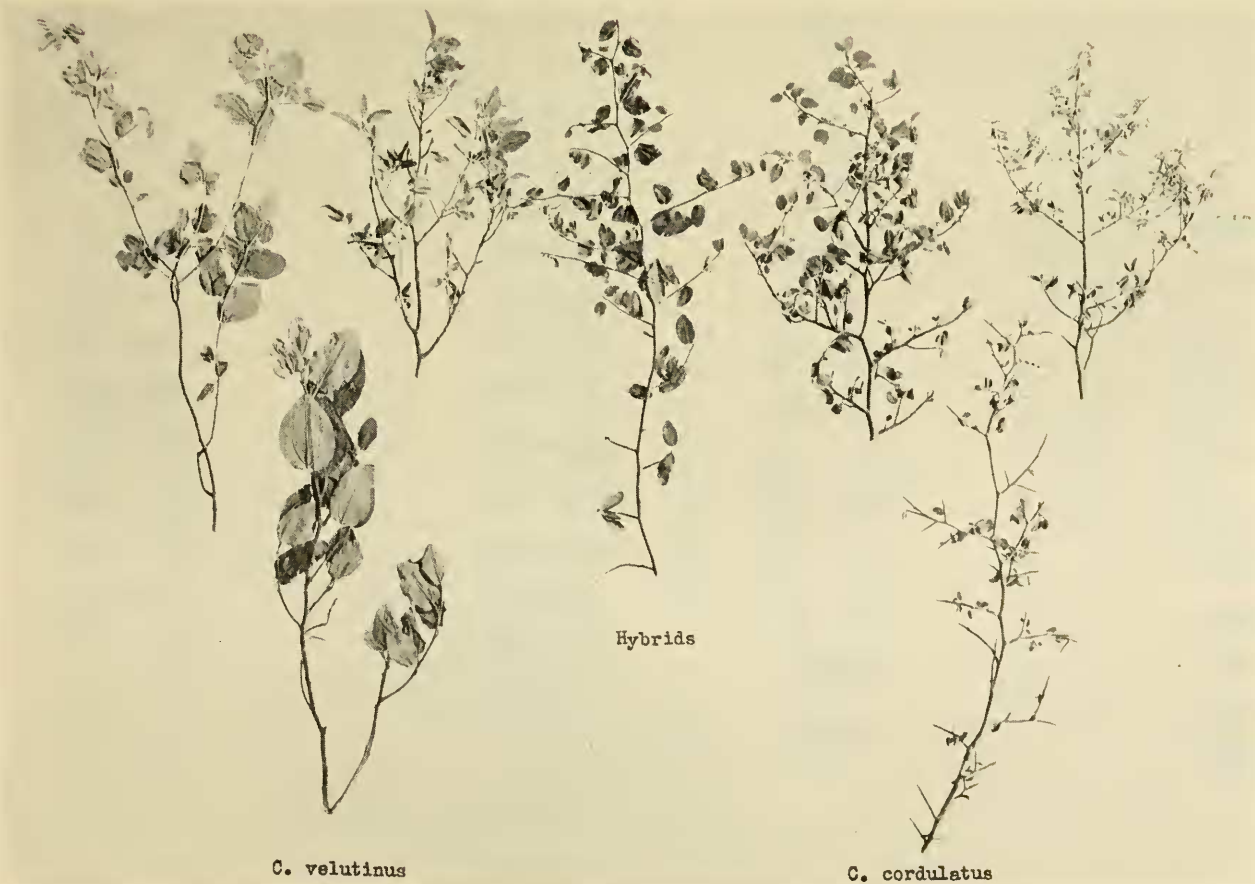

C. velutinus
Hybrids
C. cordulatus

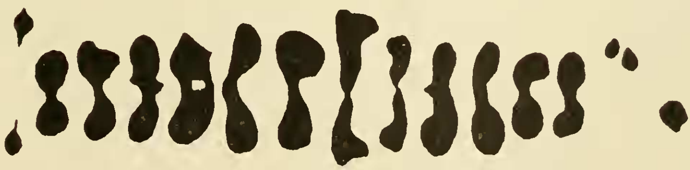
PLATE 33

Chromosomes of *C. cordulatus*, *C. velutinus*, and of the hybrid × *C. Lorenzenii*. *C. cordulatus*, Nobs 76, Snow Flat, elevation 4500 feet, Nevada County, California; 12 regular pairs. *C. velutinus*, Nobs 79, Agate Bay, Lake Tahoe, Placer County, California; 12 regular pairs. × *C. Lorenzenii*, Nobs 117, Observation Point, Lake Tahoe, Eldorado County, California; 12 regular pairs. × *C. Lorenzenii*, Nobs 118, Observation Point, Lake Tahoe, Eldorado County, California; 12 regular pairs, one very small pair, and 3 fragments.

C. cordulatus

No. 117 

x C. Lorenzenii

No. 118 

C. velutinus

PLATE 34

Photographs of specimens of *C. thyrsiflorus*, *C. papillosus*, and a graded series of five of their hybrids taken from an area where the two species occur together.


Hybrids
C. thyrsiflorus
C. papillosus

PLATE 35

Photographs of specimens of *C. prostratus*, *C. cuneatus*, and a graded series of four of their hybrids taken from an area where the two species occur together.


Hybrids
C. prostratus
C. cuneatus

PLATE 36

Diagrams of the growth forms of *C. prostratus*, *C. cuneatus*, and one of their hybrids.


C. prostratus
hybrid
C cuneatus